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Prominence of delta oscillatory rhythms in the motor cortex and their relevance for auditory and speech perception

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Highlights

- Delta (0.5-4 Hz) oscillations are endogenous rhythms of the motor system and can be generated independently from motor beta oscillations.
- Motor delta oscillations encode neural motor trajectories, coordinate articulatory movements and are visible in the dynamics of most basic motor acts.
- Motor delta oscillations encode sensory temporal contextual information and in return shape sensory processes by imposing temporal constraints on the sampling of sensory information.
- Motor delta oscillations optimize the parsing, encoding and processing of slow linguistic information.

Abstract

In the motor cortex, beta oscillations (~12-30 Hz) are generally considered a principal rhythm contributing to movement planning and execution. Beta oscillations cohabit and dynamically interact with slow delta oscillations (0.5-4 Hz), but the role of delta oscillations and the subordinate relationship between these rhythms in the perception-action loop remains unclear. Here, we review evidence that motor delta oscillations shape the dynamics of motor behaviors and sensorimotor processes, in particular during auditory perception. We describe the functional coupling between delta and beta oscillations in the motor cortex during spontaneous and planned motor acts. In an active sensing framework, perception is strongly shaped by motor activity, in particular in the delta band, which imposes temporal constraints on the sampling of sensory information. By encoding temporal contextual information, delta oscillations modulate auditory processing and impact behavioral outcomes. Finally, we consider the contribution of motor delta oscillations in the perceptual analysis of speech signals, providing a contextual temporal frame to optimize the parsing and processing of slow linguistic information.

Keywords: neural oscillations; delta; speech perception; audio-motor coupling; rhythm; active sensing, active inference

Intrinsic oscillatory activity in the motor cortex

Cortical rhythms reflect synchronous, periodic shifting of neuronal ensembles between high and low excitability states, that coordinates neural communication (Schroeder et al. 2008; Schroeder and Lakatos 2009; Buzsáki and Draguhn 2004; Wang 2010). In the motor cortex, the vast majority of existing data point to beta oscillations (~12-30 Hz; frequency borders based on Buzsaki 2006, p.112) as a predominant and specific rhythm during rest and to coordinate information transfer in action planning and execution (Murthy and Fetz 1992; Mellem et al. 2017; Groppe et al. 2013; Hillebrand et al. 2012; Ramkumar et al. 2014; Brookes et al. 2011). Spectral peaks in the beta band visibly stand out in frequency-domain representations of neural recordings of cortical motor areas, when analysed during cognitive tasks or rest (e.g., Keitel and Gross 2016; Shin et al. 2017; Haegens et al. 2011; Hillebrand et al. 2012). However, using finer-grained spectral analysis methods to analyze recordings from the motor cortex reveals a much more complex picture (Keitel and Gross 2016; Groppe et al. 2013; Hall et al. 2014). In humans, for instance, the analysis of ongoing oscillatory activity of the primary motor cortex (bilateral precentral gyrus) is characterized by consistent spectral peaks, principally in the delta (0.5-4 Hz) and beta frequency ranges (**Figure 1**; (Keitel and Gross 2016).

Interestingly, a wealth of experimental studies have supported the notion that these oscillatory rhythms can be hierarchically structured in time (Schroeder et al. 2008; Schroeder and Lakatos 2009; Buzsáki and Draguhn 2004), with a large variety of possible types of cross-frequency coupling (phase-phase, phase-amplitude etc.). Although arguably the most common type is a phase-amplitude coupling between theta (4-8 Hz) and high-gamma (80-150 Hz) bands respectively (e.g. Canolty et al. 2006), recent evidence has revealed the same type of cross-frequency relationship between the phase of delta- and power of beta-oscillations in the motor cortex. For example, a functionally relevant delta-beta phase-amplitude coupling has been shown in the motor cortex during auditory (Morillon and Baillet 2017; Arnal et al. 2015; Keitel et al. 2018) and visual (Saleh et al. 2010) perception: This specific spectro-spatial pattern of activity represents temporal information and is directly related to participants' behavioural outcome in tasks involving temporal processing (see below). Whether delta and beta rhythms are intrinsically inter-related or whether they can occur independently remains to be formally determined. Studying how brain oscillations occur over time during rest, a recent study (Keitel and Gross 2016) showed that while delta oscillations in the motor cortex tend to co-occur with beta oscillations (red lines in **Figure 1**), beta activity (yellow lines) can occur independently of delta activity. Both in vitro modelling (Carracedo et al. 2013) and empirical studies (Lakatos et al. 2005; Hall et al. 2014) however indicate that neocortical local circuits can generate delta rhythms without concurrent beta activity. Studying the occurrence of delta rhythms in the monkey motor system, there is also clear-cut evidence that reliable delta oscillatory patterns intervene in various states (while performing a motor task, as well as during sleep and sedation) and that these delta patterns can occur independently of beta oscillations (Hall et al. 2014). While computational studies provide compelling neurophysiological and functional models for the generation of sensorimotor beta rhythms (Sherman et al. 2016; Lee et al. 2013), how motor delta rhythms emerge remains poorly understood. The asymmetrical relationship between delta and beta rhythms needs to be further characterized at the cellular and network level, in particular to understand how these two rhythms are generated cortically and whether/when they emerge from distinct versus overlapping circuits (Hyafil et al. 2015; Carracedo et al. 2013; Shin et al. 2017).

Delta oscillations have been traditionally associated with resting functions such as deep sleep and memory consolidation (Huber et al. 2004). However, multiple findings converge to support the relevance of intrinsic delta oscillations at the functional and behavioral levels, where rhythmicity, i.e. periodic recurrences, are observed. For instance, a most basic motor act, walking, is intrinsically rhythmic and operates within the delta range (2 Hz; MacDougall and Moore 2005), strikingly mirroring spontaneous motor oscillatory activity (see the deviation at ~2 Hz from the 1/f distribution of delta activity in **Figure 1**). Spontaneous motor rhythmic behaviors such as finger tapping operate at a preferred tempo of ~1.5-2 Hz, and motor tapping has an optimal temporal precision within the range of ~0.8-2.5 Hz (Fraisse 1982; Moelants 2002; McAuley 2010; Repp and Su 2013). Moreover, during production of complex motor behaviors such as speech, the coordination of articulatory movements is encoded in kinematics trajectories characterized by damped oscillatory dynamics (Chartier et al. 2018). And even during non-periodic motor behaviors, such as reaching, motor trajectories are encoded in neural dynamical patterns that oscillate around 1-2 Hz (Churchland et al. 2012; Sussillo et al. 2015; Hall et al. 2014). Delta oscillations in the motor cortex also anticipate the timing of informative cues in a motor planning task (Saleh et al. 2010), facilitate coherence between motor and parietal regions during decision making (Nácher et al. 2013), organize oscillatory activity in the cortico-striatal network (López-Azcárate et al. 2013), and predict hand selection for reaching (Hamel-Thibault et al. 2018). Thus, motor delta oscillations shape the dynamics of motor behaviors and motor neural processes.

Rhythmic sampling of perceptual information

In an active sensing framework, perception is shaped by motor dynamics (Morillon et al. 2015). Indeed, our sensory organs are not passive receptacles for stimulation but are part of an action-perception closed-loop system (Kleinfeld et al. 2006; Schroeder et al. 2010; Ahissar and Assa 2016; Rajkai et al. 2008; Barczak et al. 2019). Consequently, motor acts and associated oscillatory dynamics temporally structure the activity of sensory cortices, and, as a consequence, the processing of incoming sensory inputs. Corollary discharge signals provided by motor areas to sensory processing also convey system-specific content information (spatial, spectral, etc.) as well as its underlying temporal frame (i.e., contextual temporal information; Crapse and Sommer 2008). Hence, temporal sampling of perceptual information is not restricted to the rhythms of overt actions but is also shaped by covert motor and/or attentional dynamics. As exemplified by whisking and sniffing in rodents and saccadic sampling during free viewing in primates, our motor-driven information sampling routines follow periodic patterns (Crochet et al. 2011; Wachowiak 2011; McAuley et al. 1999). Each sensing organ alternates between operational modes, characterized respectively by low (delta) and high (>4 Hz) modal frequencies: 1-2 vs. 6-12 Hz for olfaction (respiration vs. sniffing in rodents; Wachowiak 2011), 1-5 vs. 5-20 Hz for somatosensation (whiskers' wakefulness vs. exploration in rodents; Crochet et al. 2011), 3 vs. 10-12 Hz for vision (fixational microsaccades vs. saccadic search in both human and non-human primates; McAuley et al. 1999; Bosman et al. 2009; Ahissar and Arieli 2012). These rhythmic tendencies are sufficiently conserved, so that characteristic intrinsic time courses associated stems for overtly controlling perception impose periodicity even during covert sampling of the environment: On the one hand, in the auditory domain –where overt active sensing appears to be lacking (as bottom-up auditory processing is remarkably divorced from movements; (Schroeder et al. 2010; Morillon et al.

2015)–, recent frameworks describe a covert form of active sensing, whereby oscillatory influences from motor cortex modulate activity in auditory regions during perception (see below; Arnal 2012; Patel and Iversen 2014; Morillon et al. 2015; Merchant et al. 2015). On the other hand, during visual sustained spatial attention, fronto-parietal network-level interactions organize environmental sampling of visual regions outside the attentional focus into rhythmic cycles (Fiebelkorn et al. 2018; see also VanRullen 2016). In regard to delta activity, the accumulation of visual evidence during perceptual decision making is also constrained by a serial processing bottleneck operating in the delta (~2 Hz) range (Wyart et al. 2012). Delta-range oscillatory dynamics are even argued to be responsible for phenomena such as attentional blink, inhibition of return and the psychological refractory period (Wyart et al. 2012; Schroeder and Lakatos 2009). Overall, intrinsic (motor and attentional) neural dynamics thus appear to impose a temporal frame that constrains perceptual sampling in time. Future models and experiments need to investigate how these multiple neural structures –devoted to specific algorithmic processes and having specific temporal constraints– are dynamically coordinated to subserve or facilitate perceptual processing.

Temporal predictions in auditory attention

When sensory signals hold a recurring temporal structure, they enable a proactive and temporally selective preparation for anticipated relevant events (Nobre and van Ede 2018; Rimmele et al. 2018). Acoustic signals such as speech and music exhibit reliable temporal regularities that can be used to generate temporal predictions (Ding et al. 2017). Behavioral experiments demonstrate that anticipating the temporal occurrence of an upcoming event optimizes its processing by improving the quality of auditory information (Jaramillo and Zador 2011; Morillon et al. 2016; Wollman and Morillon 2018). This enhancement correlates with the reorganisation of low-frequency neural oscillations, which temporally modulates the excitability of task-relevant neural populations, and thus act as instruments of sensory selection (Cravo, Rohenkohl, Wyart, & Nobre, 2013; Schroeder & Lakatos, 2009; Stefanics et al., 2010; (Lakatos et al. 2008). This neural reorganisation is not only visible in sensory cortices, but also in a distinct network of areas including posterior parietal, inferior motor, inferior frontal and superior midline frontal cortex (Besle et al. 2011).

Recently, attentional modulation of auditory information was shown to depend on the downward propagation of temporal predictions, which originate at least in part in the motor cortex (Morillon and Baillet 2017). Temporal information is represented in the motor cortex in delta-beta phase-amplitude coupled oscillations (**Figure 2A**; Saleh et al. 2010; Arnal et al. 2015; Morillon and Baillet 2017), and both delta phase and beta amplitude seem to modulate auditory processing and predict behavioral outcome (**Figure 2**; Iversen et al. 2009; Stefanics et al. 2010; Arnal and Kleinschmidt 2017; Morillon and Baillet 2017). It was recently proposed that time estimation relies on the neural recycling of action circuits and is implemented by internal, non-conscious ‘simulation’ of movements in most ecological situations (Coull 2011; Arnal 2012; Arnal and Giraud 2012; Schubotz 2007). This idea mirrors the central proposition of the premotor theory of attention, that covert shifts in spatial attention utilize much of the same fronto-parieto-collicular circuitry that controls overt shifts in eye position (Rizzolatti et al. 1987). In this view, the transmission of temporal information from motor to auditory regions could be implemented through corollary discharge signals (Crapse and Sommer 2008).

However, the route(s) by which activity in motor areas may modulate auditory processing and perception remain currently unknown (Morillon et al. 2015). Despite these uncertainties, overall, these results indicate that motor delta oscillations play a key functional role in human auditory perception, both enabling and constraining the temporal flow of information.

Motor contributions to speech perception

Human speech is in essence structured in the temporal dimension, with nested dynamics organized according to a hierarchy of linguistic timescales (phoneme, syllable, word, phrase; (Giraud and Poeppel 2012; Ding et al. 2016; Keitel et al. 2018; Schroeder et al. 2008). Although speech is not strictly periodic, its regularities are visible as peaks in the power and modulation spectrum of the speech envelope (Ding et al. 2017; Keitel et al. 2018). Remarkably, these acoustic dynamics are mirrored by neural dynamics at similar timescales (e.g., ~4-5 Hz for syllabic and theta rates; ~1-2 Hz for phrasal and delta rates) and this hierarchy of neural processes seems to underlie grammar-based internal construction of hierarchical linguistic structure (Ding et al. 2016). It is currently debated whether these low-frequency auditory neural dynamics reflect the involvement of oscillatory processes in speech perception, or solely a succession of evoked responses or of another type of non-linear filtering process. However, during perception of (western) music, which has a salient main modulation rate around 2 Hz (Ding et al. 2017), brain responses at the delta rate are best modelled with both components of bottom-up evoked responses and internal oscillatory synchronization (Doelling et al. 2019). Auditory neural dynamics are moreover modulated in a proactive and temporally flexible manner by higher-order regions which convey temporal or linguistic predictions of the sensory input (Barczak et al. 2018; Morillon and Baillet 2017; Gagnepain et al. 2012; Rimmele et al. 2018). This combination of local oscillatory and top-down modulatory processes could underlie the auditory tracking of the non purely-periodic speech signal (Rimmele et al. 2018).

In spoken languages, prosodic information (intonation, pauses) naturally fluctuates around 0.5-3 Hz (i.e., in the delta range) and encompasses phrasal and word-level linguistic units (Ghitza 2017). Recent research has highlighted the distinctive role of delta rate dynamics in the temporal cortex for prosodic tracking and high-level linguistic processes (Bourguignon et al. 2013; Vander Ghinst et al. 2016; Ding et al. 2016; Keitel et al. 2018; Kösem and van Wassenhove 2017; Molinaro and Lizarazu 2018). Strikingly, during speech perception, spontaneous finger tapping at the perceived (prosodic) rhythm of speech occurs within the delta range (i.e. at ~2.5 Hz, c.f. Lidji et al. 2011). A similar effect is visible during music perception, with spontaneous movements occurring at the perceived beat, around 0.5-4 Hz (Rajendran et al. 2018; Merchant et al. 2015). These findings point toward a preference of attentional or motor systems for the slow temporal dynamics of auditory streams. Accordingly, neuroimaging studies show that during speech processing, delta oscillations are not only visible in temporal areas, but also in the motor cortex. Delta motor cortical dynamics uniquely contribute to both the modulation of auditory processing and comprehension. On the one hand, the tracking of acoustic dynamics by the (left) auditory cortex is principally modulated by motor areas, through delta (and to a lesser extent theta) oscillatory activity (Park et al. 2015; Keitel et al. 2017). On the other hand, in motor areas, both delta-tracking of the phrasal acoustic rate and delta-beta coupling predicts speech comprehension (**Figure 3**; Keitel et al.

2018). Speech also relies on other rhythms, notably the 4-5 Hz main acoustic modulation generated by mouth movements (Chandrasekaran et al. 2009; Ding et al. 2017), which also couples auditory and motor cortical areas during speech perception (Assaneo and Poeppel 2018). These different sensorimotor rhythms seem to have different functional contributions during speech perception (Cogan and Poeppel 2011), but their respective role is currently unclear.

Overall, this indicates that one of the contributions of the motor cortex to speech processing is the analysis of the slow temporal dynamics of the speech signal, likely providing a contextual temporal frame to (at least) distant auditory regions that parse linguistic information, thereby improving the quality of speech processing. The specific contribution of motor areas to speech perception is a matter of debate which has been mostly investigated with regard to its role in the processing of phonetic features or phonological or lexico-semantic information (Hickok et al. 2011; Schomers and Pulvermüller 2016; Skipper et al. 2017; Pulvermüller 2018). However, these recent results crucially reveal its unique role in the analysis of speech temporal dynamics, a factor which has been mostly overlooked until now (Scott et al. 2009). This contribution of motor areas in the analysis of perceptual temporal dynamics is likely modality- and domain- general and would occur during perception of any sensory signal temporally structured with low-frequency dynamics, although it is currently unclear whether speech-specific (e.g. semantic or syntactic) processes can *additionally* contribute to motor temporal predictions. For example, top-down information from orbitofrontal areas is conveyed to motor areas during speech perception, which is a potential mechanism by which the motor cortex could receive speech-specific information (Keitel et al. 2017). Furthermore, a perceptually relevant, speech-specific function of motor predictions might be to anticipate the end of a speaker's turn to facilitate smooth turn-taking in conversations (Scott et al. 2009; Wilson and Wilson 2005).

Conclusions

The studies reviewed above provide evidence that delta oscillations are intrinsic in the motor cortex and critically shape both overt motor behaviors and covert motor-related modulation of sensory neural processes. They reflect a behavioral time-constant that is directly interpretable in a cognitive framework. This delta motor activity often seems to be intrinsically linked to beta oscillations through cross-frequency coupling, but the relationship between delta and beta rhythms is dynamic and still needs to be further characterized at the local cell circuit and network levels. However, there is emerging evidence that delta oscillations can be generated independently from beta oscillations (Carracedo et al. 2013; Hall et al. 2014). Motor delta oscillations control perceptual sampling by providing a temporal frame that both amplifies and orders sensory processing. Such effects are particularly striking during perception of temporally structured sensory signals such as speech. While the evidence we have considered indicates that the motor cortex is a constitutive part of the 'auditory system', the mechanisms and pathways controlling the gain of auditory processing and perception is currently unclear. In particular, while the primary motor, somatosensory, and auditory cortex seem to be strongly interconnected (Skipper and Hasson 2017), evidence of direct projections between motor and auditory regions in humans is currently lacking (Morillon et al. 2015). Importantly, multiple neural structures related to motor or attentional (Fiebelkorn et al. 2018;

Wyart et al. 2012) processes temporally constrain sensory processing. Understanding their interrelation in terms of system dynamics represents a major challenge. Delta oscillations are not unique to the motor cortex or to auditory perception. Rather, intrinsic spontaneous delta activity is also found in more inferior and anterior frontal areas (Mellem et al. 2017; Keitel and Gross 2016) and is demonstrably involved in thalamo-cortical interactions (Barczak et al. 2018; Steriade et al. 1993; Timofeev and Steriade 1996). Outside of the realm of sleep, it is unknown whether and how these delta rhythms are related to each other, and it is not yet clear why all of these areas spontaneously oscillate at this rate.

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References

Ahissar, E. and Arieli, A. 2012. Seeing via miniature eye movements: A dynamic hypothesis for vision. *Frontiers in Computational Neuroscience* 6, p. 89.

Ahissar, E. and Assa, E. 2016. Perception as a closed-loop convergence process. *eLife* 5.

Arnal, L.H. 2012. Predicting “When” Using the Motor System’s Beta-Band Oscillations. *Frontiers in Human Neuroscience* 6, p. 225.

Arnal, L.H., Doelling, K.B. and Poeppel, D. 2015. Delta-Beta Coupled Oscillations Underlie Temporal Prediction Accuracy. *Cerebral Cortex* 25(9), pp. 3077–3085.

Arnal, L.H. and Giraud, A.-L. 2012. Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences* 16(7), pp. 390–398.

Arnal, L.H. and Kleinschmidt, A.K. 2017. Entrained delta oscillations reflect the subjective tracking of time. *Communicative & Integrative Biology* 10(5–6), p. e1349583.

Assaneo, M.F. and Poeppel, D. 2018. The coupling between auditory and motor cortices is rate-restricted: Evidence for an intrinsic speech-motor rhythm. *Science advances* 4(2), p. eaao3842.

Barczak, A., Haegens, S., Ross, D.A., McGinnis, T., Lakatos, P. and Schroeder, C.E. 2019. Dynamic Modulation of Cortical Excitability during Visual Active Sensing. *Cell reports* 27(12), pp. 3447-3459.e3.

Barczak, A., O’Connell, M.N., McGinnis, T., et al. 2018. Top-down, contextual entrainment of neuronal oscillations in the auditory thalamocortical circuit. *Proceedings of the National Academy of Sciences of the United States of America* 115(32), pp. E7605–E7614.

Besle, J., Schevon, C.A., Mehta, A.D., et al. 2011. Tuning of the human neocortex to the temporal dynamics of attended events. *The Journal of Neuroscience* 31(9), pp. 3176–3185.

Bosman, C.A., Womelsdorf, T., Desimone, R. and Fries, P. 2009. A microsaccadic rhythm modulates gamma-band synchronization and behavior. *The Journal of Neuroscience* 29(30), pp. 9471–9480.

Bourguignon, M., De Tiège, X., de Beeck, M.O., et al. 2013. The pace of prosodic phrasing couples the listener’s cortex to the reader’s voice. *Human Brain Mapping* 34(2), pp. 314–326.

Brookes, M.J., Woolrich, M., Luckhoo, H., et al. 2011. Investigating the electrophysiological basis of resting state networks using magnetoencephalography. *Proceedings of the National Academy of Sciences of the United States of America* 108(40), pp. 16783–16788.

Buzsaki, G. 2006. *Rhythms of the Brain*. Oxford University Press.

Buzsáki, G. and Draguhn, A. 2004. Neuronal oscillations in cortical networks. *Science* 304(5679), pp. 1926–1929.

Canolty, R.T., Edwards, E., Dalal, S.S., et al. 2006. High gamma power is phase-locked to theta oscillations in human neocortex. *Science* 313(5793), pp. 1626–1628.

Carracedo, L.M., Kjeldsen, H., Cunnington, L., et al. 2013. A neocortical delta rhythm facilitates reciprocal interlaminar interactions via nested theta rhythms. *The Journal of Neuroscience* 33(26), pp. 10750–10761.

Chandrasekaran, C., Trubanova, A., Stillittano, S., Caplier, A. and Ghazanfar, A.A. 2009. The natural statistics of audiovisual speech. *PLoS Computational Biology* 5(7), p. e1000436.

Chartier, J., Anumanchipalli, G.K., Johnson, K. and Chang, E.F. 2018. Encoding of articulatory kinematic trajectories in human speech sensorimotor cortex. *Neuron* 98(5), pp. 1042-1054.e4.

Churchland, M.M., Cunningham, J.P., Kaufman, M.T., et al. 2012. Neural population dynamics during reaching. *Nature* 487(7405), pp. 51–56.

Cogan, G.B. and Poeppel, D. 2011. A mutual information analysis of neural coding of speech by low-frequency MEG phase information. *Journal of Neurophysiology* 106(2), pp. 554–563.

Coull, J.T. 2011. Discrete neuroanatomical substrates for generating and updating temporal expectations. In: *Space, time and number in the brain*. Elsevier, pp. 87–101.

Crapse, T.B. and Sommer, M.A. 2008. Corollary discharge across the animal kingdom. *Nature Reviews. Neuroscience* 9(8), pp. 587–600.

Crochet, S., Poulet, J.F.A., Kremer, Y. and Petersen, C.C.H. 2011. Synaptic mechanisms underlying sparse coding of active touch. *Neuron* 69(6), pp. 1160–1175.

Ding, N., Melloni, L., Zhang, H., Tian, X. and Poeppel, D. 2016. Cortical tracking of hierarchical linguistic structures in connected speech. *Nature Neuroscience* 19(1), pp. 158–164.

Ding, N., Patel, A.D., Chen, L., Butler, H., Luo, C. and Poeppel, D. 2017. Temporal modulations in speech and music. *Neuroscience and Biobehavioral Reviews* 81(Pt B), pp. 181–187.

Doelling, K.B., Assaneo, M.F., Bevilacqua, D., Pesaran, B. and Poeppel, D. 2019. An oscillator model better predicts cortical entrainment to music. *Proceedings of the National Academy of Sciences of the United States of America* 116(20), pp. 10113–10121.

Fiebelkorn, I.C., Pinsk, M.A. and Kastner, S. 2018. A Dynamic Interplay within the Frontoparietal Network Underlies Rhythmic Spatial Attention. *Neuron* 99(4), pp. 842-853.e8.

Fraisse, P. 1982. Rhythm and Tempo. In: *Psychology of Music*. Elsevier, pp. 149–180.

Gagnepain, P., Henson, R.N. and Davis, M.H. 2012. Temporal predictive codes for spoken words in auditory cortex. *Current Biology* 22(7), pp. 615–621.

Ghitza, O. 2017. Acoustic-driven delta rhythms as prosodic markers. *Language, cognition and neuroscience* 32(5), pp. 545–561.

Giraud, A.-L. and Poeppel, D. 2012. Cortical oscillations and speech processing: emerging computational principles and operations. *Nature Neuroscience* 15(4), pp. 511–517.

Groppe, D.M., Bickel, S., Keller, C.J., et al. 2013. Dominant frequencies of resting human brain activity as measured by the electrocorticogram. *Neuroimage* 79, pp. 223–233.

Haegens, S., Nácher, V., Hernández, A., Luna, R., Jensen, O. and Romo, R. 2011. Beta oscillations in the monkey sensorimotor network reflect somatosensory decision making. *Proceedings of the National Academy of Sciences of the United States of America* 108(26), pp. 10708–10713.

Hall, T.M., de Carvalho, F. and Jackson, A. 2014. A common structure underlies low-frequency cortical dynamics in movement, sleep, and sedation. *Neuron* 83(5), pp. 1185–1199.

Hamel-Thibault, A., Thénault, F., Whittingstall, K. and Bernier, P.-M. 2018. Delta-Band Oscillations in Motor Regions Predict Hand Selection for Reaching. *Cerebral Cortex* 28(2), pp. 574–584.

Hickok, G., Houde, J. and Rong, F. 2011. Sensorimotor integration in speech processing: computational basis and neural organization. *Neuron* 69(3), pp. 407–422.

Hillebrand, A., Barnes, G.R., Bosboom, J.L., Berendse, H.W. and Stam, C.J. 2012. Frequency-dependent functional connectivity within resting-state networks: an atlas-based MEG beamformer solution. *Neuroimage* 59(4), pp. 3909–3921.

Huber, R., Ghilardi, M.F., Massimini, M. and Tononi, G. 2004. Local sleep and learning. *Nature* 430(6995), pp. 78–81.

Hyafil, A., Fontolan, L., Kabdebon, C., Gutkin, B. and Giraud, A.-L. 2015. Speech encoding by coupled cortical theta and gamma oscillations. *eLife* 4, p. e06213.

Iversen, J.R., Repp, B.H. and Patel, A.D. 2009. Top-down control of rhythm perception modulates early auditory responses. *Annals of the New York Academy of Sciences* 1169, pp. 58–73.

Jaramillo, S. and Zador, A.M. 2011. The auditory cortex mediates the perceptual effects of acoustic temporal expectation. *Nature Neuroscience* 14(2), pp. 246–251.

Keitel, A. and Gross, J. 2016. Individual Human Brain Areas Can Be Identified from Their Characteristic Spectral Activation Fingerprints. *PLoS Biology* 14(6), p. e1002498.

Keitel, A., Gross, J. and Kayser, C. 2018. Perceptually relevant speech tracking in auditory and motor cortex reflects distinct linguistic features. *PLoS Biology* 16(3), p. e2004473.

Keitel, A., Ince, R.A.A., Gross, J. and Kayser, C. 2017. Auditory cortical delta-entrainment interacts with oscillatory power in multiple fronto-parietal networks. *Neuroimage* 147, pp. 32–42.

Kleinfeld, D., Ahissar, E. and Diamond, M.E. 2006. Active sensation: insights from the rodent vibrissa sensorimotor system. *Current Opinion in Neurobiology* 16(4), pp. 435–444.

Kösem, A. and van Wassenhove, V. 2017. Distinct contributions of low- and high-frequency neural oscillations to speech comprehension. *Language, cognition and neuroscience* 32(5), pp. 536–544.

Lakatos, P., Karmos, G., Mehta, A.D., Ulbert, I. and Schroeder, C.E. 2008. Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science* 320(5872), pp. 110–113.

Lakatos, P., Shah, A.S., Knuth, K.H., Ulbert, I., Karmos, G. and Schroeder, C.E. 2005. An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *Journal of Neurophysiology* 94(3), pp. 1904–1911.

Lee, J.H., Whittington, M.A. and Kopell, N.J. 2013. Top-down beta rhythms support selective attention via interlaminar interaction: a model. *PLoS Computational Biology* 9(8), p. e1003164.

Lidji, P., Palmer, C., Peretz, I. and Morningstar, M. 2011. Listeners feel the beat: entrainment to English and French speech rhythms. *Psychonomic Bulletin & Review* 18(6), pp. 1035–1041.

López-Azcárate, J., Nicolás, M.J., Cordon, I., Alegre, M., Valencia, M. and Artieda, J. 2013. Delta-mediated cross-frequency coupling organizes oscillatory activity across the rat cortico-basal ganglia network. *Frontiers in Neural Circuits* 7, p. 155.

MacDougall, H.G. and Moore, S.T. 2005. Marching to the beat of the same drummer: the spontaneous tempo of human locomotion. *Journal of Applied Physiology* 99(3), pp. 1164–1173.

McAuley, J.D. 2010. Tempo and Rhythm. In: Riess Jones, M., Fay, R. R., and Popper, A. N. eds. *Music Perception*. Springer handbook of auditory research. New York, NY: Springer New York, pp. 165–199.

McAuley, J.H., Rothwell, J.C. and Marsden, C.D. 1999. Human anticipatory eye movements may reflect rhythmic central nervous activity. *Neuroscience* 94(2), pp. 339–350.

Mellem, M.S., Wohltjen, S., Gotts, S.J., Ghuman, A.S. and Martin, A. 2017. Intrinsic frequency biases and profiles across human cortex. *Journal of Neurophysiology* 118(5), pp. 2853–2864.

Merchant, H., Grahn, J., Trainor, L., Rohrmeier, M. and Fitch, W.T. 2015. Finding the beat: a neural perspective across humans and non-human primates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 370(1664), p. 20140093.

Moelants, D. 2002. Preferred tempo reconsidered. *Proceedings of the 7th international conference on music perception and cognition* 2002, p. 1.

Molinaro, N. and Lizarazu, M. 2018. Delta(but not theta)-band cortical entrainment involves speech-specific processing. *The European Journal of Neuroscience* 48(7), pp. 2642–2650.

Morillon, B. and Baillet, S. 2017. Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences of the United States of America* 114(42), pp. E8913–E8921.

Morillon, B., Hackett, T.A., Kajikawa, Y. and Schroeder, C.E. 2015. Predictive motor control of sensory dynamics in auditory active sensing. *Current Opinion in Neurobiology* 31, pp. 230–238.

Morillon, B., Schroeder, C.E., Wyart, V. and Arnal, L.H. 2016. Temporal Prediction in lieu of Periodic Stimulation. *The Journal of Neuroscience* 36(8), pp. 2342–2347.

Murthy, V.N. and Fetz, E.E. 1992. Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving

monkeys. *Proceedings of the National Academy of Sciences of the United States of America* 89(12), pp. 5670–5674.

Nácher, V., Ledberg, A., Deco, G. and Romo, R. 2013. Coherent delta-band oscillations between cortical areas correlate with decision making. *Proceedings of the National Academy of Sciences of the United States of America* 110(37), pp. 15085–15090.

Nobre, A.C. and van Ede, F. 2018. Anticipated moments: temporal structure in attention. *Nature Reviews. Neuroscience* 19(1), pp. 34–48.

Park, H., Ince, R.A.A., Schyns, P.G., Thut, G. and Gross, J. 2015. Frontal top-down signals increase coupling of auditory low-frequency oscillations to continuous speech in human listeners. *Current Biology* 25(12), pp. 1649–1653.

Patel, A.D. and Iversen, J.R. 2014. The evolutionary neuroscience of musical beat perception: the Action Simulation for Auditory Prediction (ASAP) hypothesis. *Frontiers in Systems Neuroscience* 8, p. 57.

Pulvermüller, F. 2018. Neural reuse of action perception circuits for language, concepts and communication. *Progress in Neurobiology* 160, pp. 1–44.

Rajendran, V.G., Teki, S. and Schnupp, J.W.H. 2018. Temporal Processing in Audition: Insights from Music. *Neuroscience* 389, pp. 4–18.

Rajkai, C., Lakatos, P., Chen, C.-M., Pincze, Z., Karmos, G. and Schroeder, C.E. 2008. Transient cortical excitation at the onset of visual fixation. *Cerebral Cortex* 18(1), pp. 200–209.

Ramkumar, P., Parkkonen, L. and Hyvärinen, A. 2014. Group-level spatial independent component analysis of Fourier envelopes of resting-state MEG data. *Neuroimage* 86, pp. 480–491.

Repp, B.H. and Su, Y.-H. 2013. Sensorimotor synchronization: a review of recent research (2006-2012). *Psychonomic Bulletin & Review* 20(3), pp. 403–452.

Rimmele, J.M., Morillon, B., Poeppel, D. and Arnal, L.H. 2018. Proactive sensing of periodic and aperiodic auditory patterns. *Trends in Cognitive Sciences* 22(10), pp. 870–882.

Rizzolatti, G., Riggio, L., Dascola, I. and Umiltá, C. 1987. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25(1A), pp. 31–40.

Saleh, M., Reimer, J., Penn, R., Ojakangas, C.L. and Hatsopoulos, N.G. 2010. Fast and slow oscillations in human primary motor cortex predict oncoming behaviorally relevant cues. *Neuron* 65(4), pp. 461–471.

Schomers, M.R. and Pulvermüller, F. 2016. Is the sensorimotor cortex relevant for speech perception and understanding? an integrative review. *Frontiers in Human Neuroscience* 10, p. 435.

Schroeder, C.E. and Lakatos, P. 2009. Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences* 32(1), pp. 9–18.

Schroeder, C.E., Lakatos, P., Kajikawa, Y., Partan, S. and Puce, A. 2008. Neuronal oscillations and visual amplification of speech. *Trends in Cognitive Sciences* 12(3), pp. 106–113.

Schroeder, C.E., Wilson, D.A., Radman, T., Scharfman, H. and Lakatos, P. 2010. Dynamics of Active Sensing and perceptual selection. *Current Opinion in Neurobiology* 20(2), pp. 172–176.

Schubotz, R.I. 2007. Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Sciences* 11(5), pp. 211–218.

Scott, S.K., McGettigan, C. and Eisner, F. 2009. A little more conversation, a little less action--candidate roles for the motor cortex in speech perception. *Nature Reviews. Neuroscience* 10(4), pp. 295–302.

Sherman, M.A., Lee, S., Law, R., et al. 2016. Neural mechanisms of transient neocortical beta rhythms: Converging evidence from humans, computational modeling, monkeys, and mice. *Proceedings of the National Academy of Sciences of the United States of America* 113(33), pp. E4885-94.

Shin, H., Law, R., Tsutsui, S., Moore, C.I. and Jones, S.R. 2017. The rate of transient beta frequency events predicts behavior across tasks and species. *eLife* 6.

Skipper, J.I., Devlin, J.T. and Lametti, D.R. 2017. The hearing ear is always found close to the speaking tongue: Review of the role of the motor system in speech perception. *Brain and Language* 164, pp. 77–105.

Skipper, J.I. and Hasson, U. 2017. A core speech circuit between primary motor, somatosensory, and auditory cortex: Evidence from connectivity and genetic descriptions. *BioRxiv*.

Stefanics, G., Hangya, B., Hernádi, I., Winkler, I., Lakatos, P. and Ulbert, I. 2010. Phase entrainment of human

delta oscillations can mediate the effects of expectation on reaction speed. *The Journal of Neuroscience* 30(41), pp. 13578–13585.

Steriade, M., McCormick, D.A. and Sejnowski, T.J. 1993. Thalamocortical oscillations in the sleeping and aroused brain. *Science* 262(5134), pp. 679–685.

Sussillo, D., Churchland, M.M., Kaufman, M.T. and Shenoy, K.V. 2015. A neural network that finds a naturalistic solution for the production of muscle activity. *Nature Neuroscience* 18(7), pp. 1025–1033.

Timofeev, I. and Steriade, M. 1996. Low-frequency rhythms in the thalamus of intact-cortex and decorticated cats. *Journal of Neurophysiology* 76(6), pp. 4152–4168.

Vander Ghinst, M., Bourguignon, M., Op de Beeck, M., et al. 2016. Left Superior Temporal Gyrus Is Coupled to Attended Speech in a Cocktail-Party Auditory Scene. *The Journal of Neuroscience* 36(5), pp. 1596–1606.

VanRullen, R. 2016. Perceptual Cycles. *Trends in Cognitive Sciences* 20(10), pp. 723–735.

Wachowiak, M. 2011. All in a sniff: olfaction as a model for active sensing. *Neuron* 71(6), pp. 962–973.

Wang, X.-J. 2010. Neurophysiological and computational principles of cortical rhythms in cognition. *Physiological Reviews* 90(3), pp. 1195–1268.

Wilson, M. and Wilson, T.P. 2005. An oscillator model of the timing of turn-taking. *Psychonomic Bulletin & Review* 12(6), pp. 957–968.

Wollman, I. and Morillon, B. 2018. Organizational principles of multidimensional predictions in human auditory attention. *Scientific reports* 8(1), p. 13466.

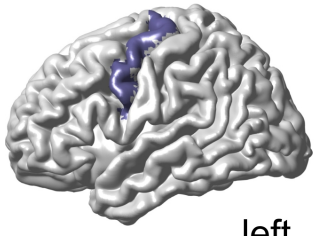
Wyart, V., de Gardelle, V., Scholl, J. and Summerfield, C. 2012. Rhythmic fluctuations in evidence accumulation during decision making in the human brain. *Neuron* 76(4), pp. 847–858.

Figure Captions

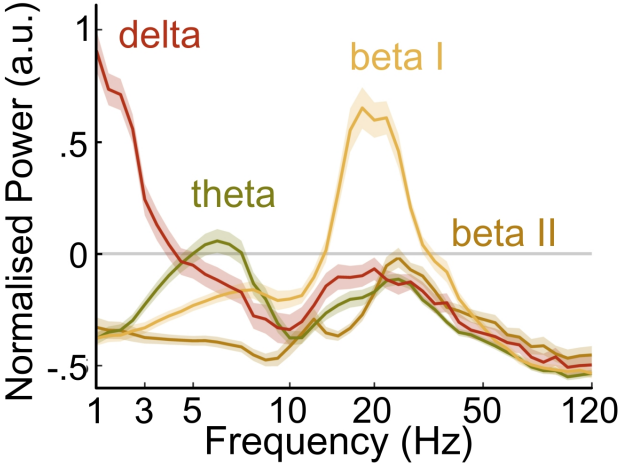
Figure 1. **Intrinsic oscillations in the motor cortex at rest** (left and right precentral gyri respectively) as captured by MEG recordings. Lines illustrate power peaks that coexist in one area but are present at different times. Dominant peaks are consistently present across participants principally in the delta and beta frequency ranges (indicated by red and yellow lines; shaded areas represent SEM across participants). Please note that delta activity follows a 1/f (power law-like) distribution across frequencies with a critical deviation at around 2 Hz, reflecting respectively neural noise and spontaneous oscillatory activity (Adapted from Keitel & Gross, 2016).

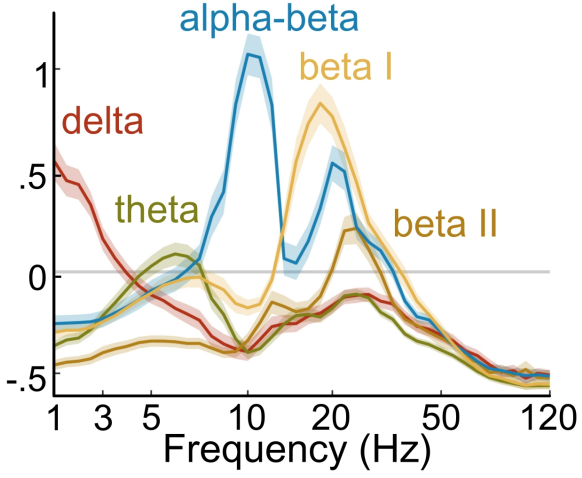
Figure 2. Temporal predictions originate in the motor cortex and are mediated by delta-beta coupled oscillations. Evidence from two magnetoencephalography experiments **A.** (top) Auditory pure tones are presented at a 3 Hz rate and covert temporal attention is modulated at 1.5 Hz (based on preceding cues). Participants have thus a stronger attentional focus toward on-beat target tones than offbeat distractors. (bottom) Temporal predictions are encoded in sensory-motor cortical regions, in the phase of delta oscillations and amplitude of beta oscillations. Finally, beta oscillations are functionally directed toward auditory regions to modulate the processing of the 3 Hz auditory input. **B.** (top) Four pure tones are presented, with the last one appearing either on-beat or offbeat (positive delay of 75 ms). (middle) Accuracy effect on the modeled time-course of delta oscillations. The black dotted line indicates the time-course of an ideal oscillation at the stationary frequency of 2 Hz (center frequency of the frequency band of interest). Blue and red lines represent the time-course of correct and incorrect conditions respectively. (bottom) Unwrapped delta phase angle during pre-stimulus time period reflects subjective duration, being larger for correctly (blue, perceived 'longer') than incorrectly (red, perceived 'normal') detected delayed trials. At target's occurrence, the phase-angle difference between correct and incorrect conditions corresponds to an 80-ms subjective time-lag (Adapted from: (A) Morillon & Baillet, 2017 and (B) Arnal & Kleinschmidt, 2017).

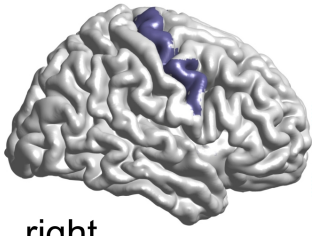
Figure 3. **Effects in the delta band that modulate speech perception in noise.** (Left) Comprehension correlates with the coupling strength between acoustic and neural dynamics at the word (~2.4 Hz) rate in temporal regions and at the phrasal (~1 Hz) rate in motor regions. (Right) In motor regions, comprehension is also impacted by (phrasal) delta-beta phase-amplitude coupling (Adapted from: Keitel et al., 2018).



left
precentral
gyrus







right
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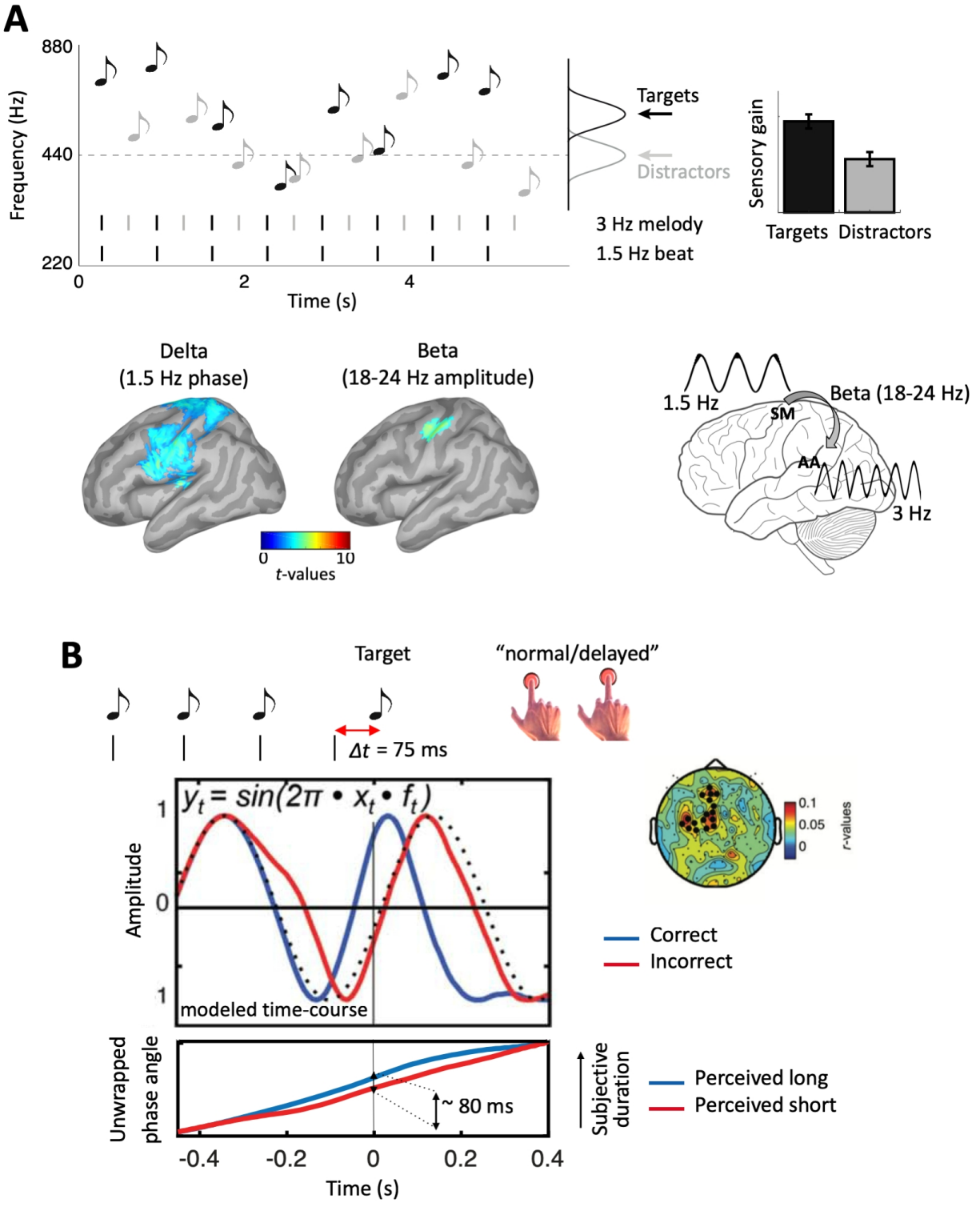
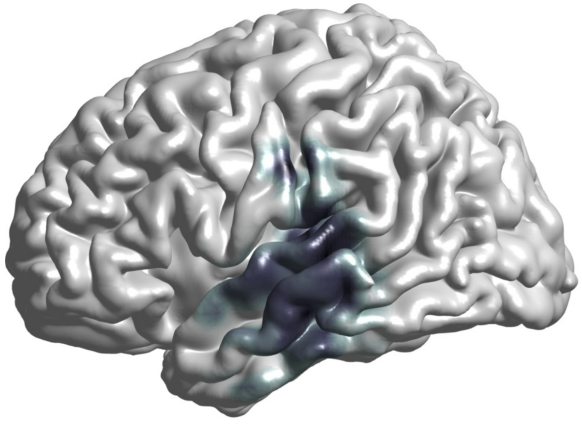
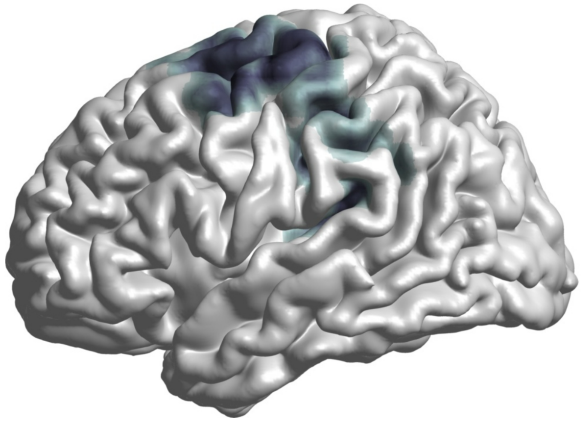

A
880
440
220
Frequency (Hz)
0
2
4
Time (s)
Targets
Distractors
3 Hz melody
1.5 Hz beat
Sensory gain
Targets
Distractors
Delta
(1.5 Hz phase)
Beta
(18-24 Hz amplitude)
0
10
t-values
1.5 Hz
Beta (18-24 Hz)
SM
AA
3 Hz
B
Target
"normal/delayed"
Δt = 75 ms
$y_t = \sin(2\pi \bullet x_t \bullet f_t)$
Amplitude
1
0
1
modeled time-course
0.1
0.05
0
r-values
Correct
Incorrect
Unwrapped
phase angle
~ 80 ms
Subjective
duration
Perceived long
Perceived short
-0.4
-0.2
0
0.2
0.4
Time (s)

Delta-tracking (words)



Delta-tracking (phrases)



Delta-beta coupling (phrases)